A QUANTITATIVE COMPARISON OF SPECIFIC AND GENERIC DIFFERENCES IN THE BETULACEAE

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With one text figure

THE CRITERIA on which the sciences of Morphology and Taxonomy are largely based have two disadvantages. They are not objective and they are not commensurable. The first of these difficulties may be resolved through improvements in morphological technique. Such simple qualitative categories as "ovate" or "obovate" are already quite as objective as the quantitative measures of chemistry or physics. Through closer analysis and more exact definition it may eventually be possible to bring the larger categories of taxonomy to a comparable degree of objectivity. Even with this improvement, the second difficulty would still remain; the categories are not reducible to a common basis. Is, for instance, the change from an ovate leaf to a lanceolate one, greater or smaller than the change from a lanceolate leaf to a linear? How do the differences between subgenera compare to generic differences on the one hand and specific differences on the other? To such questions as these the qualitative units of morphology permit no precise answers.

The following paper is a crude first attempt to work out a commensurate method for dealing with such morphological and taxonomical problems. It is an attempt to carry on consciously and mathematically the same sort of process which with a good naturalist is subconscious and unmathematical. When a naturalist distinguishes between two species which are well known to him, he subconsciously takes the component of a very large number of variables. He knows *Acer rubrum,* for instance, not by any one technical distinguishing feature, but by the total impression of a very large number of features, any one of which may vary considerably in different individuals of *Acer rubrum.* In mathematical phraseology, his generalized idea of an *Acer rubrum* is the *largest common denominator* of all the individuals he has previously recognized as belonging to that species. Any biologist who has had practical field experience with a species or a genus will probably agree with this definition. A slightly more objective demonstration will be found in a recent survey of specific differences in *Uvularia* (Anderson & Whitaker, 1934).

If such a process is to be made conscious and turned into commensurate units, we must attempt as far as possible to carry on the same sort of procedure mathematically. We must select a large number of features for measurement, features which by previous analysis are known to be individually significant, and then determine their aggregate effect mathematically. This paper is an attempt to measure the relative magnitudes of various categories in the Betulaceae by such a method. Six features are chosen and their aggregate effect is calculated by a comparatively simple method whose essential features have been described elsewhere (Anderson & Whitaker, 1934). The significance of such an index calculated from diverse components may be made clear by a comparison with well-known indices in other fields. As a measure of business activity it is common practice to combine diverse categories such as car-loadings per week, electric power output, and the price of food-stuffs. With an intrinsically meaningless scale of this type, we measure the rise and fall of business from week to week or contrast the condition in one part of the country with that in another. In just such a way there are combined in the following analysis, six features of known importance in the Betulaceae:

1: the basic chromosome number
2: the number of perigon segments in the female flower
3: the average number of stamens per flower
4: the total number of bracts in a bract-complex
5: the number of flowers per pistillate bract-complex
6: the maximum number of cell rows in the rays of the secondary xylem.

Table I shows the actual data used for the 40 species of the Betulaceae for which figures were readily available. It should be noted, however, that in the case of the perigon segments of the ovary, in the number of bracts in a bract-complex, certain factors must be taken into account. Thus there is anatomical evidence for the presence of vestigial perigon segments in the pistillate florets of some species of *Alnus* (Abbe, 1933). In the absence of a satisfactory means of indicating this mathematically they have been uniformly treated as indicated in Table I. The number of stamens per floret introduces perhaps the most variable character possessed by the members of the family. Here the data are based on representative individuals rather than on a mathematical average. These individuals have been chosen to illustrate the

TABLE I*

Genus & Species	Basic Chromo-some No.	No. of (Female) Perigon Segments	No. of Stamens per Floret	Total No. of Bracts per Staminate Bract-Complex	No. of Florets per Pistillate Bract-Complex	Maximum No. of Cell Rows in the Ray
Alnus						
§ALNOBETULA						
A. crispa	7	0	5	4	2	1
§GYMNOTHYRSUS						
A. incana	7	0	4	5	2	1
A. cordata	7	0	4	5	2	1
A. maritima	7	0	3	5	2	1
A. rhombifolia	7	0	3	5	2	3
A. hirsuta	7	0	4	5	2	1
A. rubra	7	0	4	5	2	1
Betula						
§EUBETULA						
§§COSTATAE						
B. nigra	7	0	2	3	3	4
B. utilis	7	0	2	3	3	2
B. Schmidtii	7	0	2	3	3	3
B. grossa	7	0	3	3	3	3
B. costata	7	0	3	3	3	3
B. lenta	7	0	3	3	3	4
B. lutea	7	0	3	3	3	4
§§Nanae						
B. Michauxii	7	0	1	3	1	1
B. pumila	7	0	2	3	3	3
§§Albae						
B. pendula	7	0	2	3	3	3
B. japonica	7	0	2	3	3	3
B. populifolia	7	0	2	3	3	3
B. pubescens	7	0	2	3	3	4
B. papyrifera	7	0	2	3	3	3
B. davurica	7	0	2	3	3	3
§BETULASTER						
§§ACUMINATAE						
B. Maximowicziana	7	0	3	3	3	3
B. alnoides	7	0	2	1	3	3
Corylus						
C. Avellana	7	4	2	3	2	1
C. americana	7	4	2	3	2	1
C. heterophylla	7	4	2	3	2	1
C. Colurna	7	4	2	3	2	1
C. cornuta	7	4	2	3	2	3
Ostryopsis						
O. Davidiana	8	4	2	1	2	1
Carpinus						
§DISTEGOCARPUS						
C. japonica	8	4	6	3	2	4
C. cordata	8	4	6	1	2	3
§EUCARPINUS						
C. betulus	8	4	4	1	2	4
C. caroliniana	8	4	4	1	2	3
C. laxiflora	8	4	3	1	2	3
C. Tschonoskii	8	4	3	1	2	3
C. orientalis	8	4	4	1	2	2
Ostrya						
O. virginiana	8	4	4	1	2	3
O. japonica	8	4	4	1	2	2
O. carpinifolia	8	4	3	1	2	2

*The specific names are based on Rehder (1927). The subgenera, etc., are based on Winkler (1904).

salient trends of differentiation within the group. While the number of bracts in a given staminate bract-complex is generally a relatively constant character for a genus or a species, it sometimes, as in *Alnus crispa* and *Carpinus japonica,* is variable. Here again it has been necessary to choose a significant figure, in the absence of averages. The basic chromosome numbers are taken from Woodworth (1931). The differences between species were calculated from the data in Table I by the formula:

TABLE II

SUMMARY OF INTRAGENERIC, INTRASECTIONAL DIFFERENCES

Names of Genera and Sections	Range of Differences 0-1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	5.1-6.0	6.1-7.0	Total	Av'g
ALNUS §Gymnothyrsus	10	1	4					15	1.0
BETULA §§Costatae	12	7	2					21	1.2
" §§Nanae			1					1	3.0
" §§Albae	15							15	.3
" §§Acuminatae			1					1	2.2
CORYLUS	6	4						10	0.8
CARPINUS §Distegocarpus			1					1	2.2
" §Eucarpinus	5	5						10	1.2
OSTRYA	2	1						3	1.1
SUMMARY OF INTRAGENERIC, INTERSECTIONAL DIFFERENCES									
ALNUS									
§Alnobetula—§Gymnothyrsus		4	2					6	1.8
BETULA									
§§Costatae—§§Nanae	5	4	3	2				14	2.2
" —§§Albae	29	13						42	1.0
" —§§Acuminatae	5	3	6					14	1.5
§§Nanae—§§Albae	6		5	1				12	1.6
" —§§Acuminatae	1	1		2				4	2.5
§§Albae—§§Acuminatae	5	6	1					12	1.6
CARPINUS									
§Distegocarpus—§Eucarpinus		1	6	3				10	2.9
SUMMARY OF INTERGENERIC DIFFERENCES									
ALNUS—BETULA			6	15	4			25	3.5
" —CORYLUS					18	7		25	5.0
" —OSTRYOPSIS						2	5	7	6.0
" —CARPINUS						13	12	25	6.1
" —OSTRYA						20	1	21	5.8
BETULA—CORYLUS					20	5		25	4.8
" —OSTRYOPSIS					3	14		17	5.2
" —CARPINUS					10	12	3	25	5.2
" —OSTRYA					9	16		25	5.1
CORYLUS—OSTRYOPSIS			5					5	2.4
" —CARPINUS			3	14	6	2		25	3.6
" —OSTRYA			6	9				15	3.1
OSTRYOPSIS—CARPINUS			4	1	1	1		7	3.3
" —OSTRYA		1	2					3	2.1
CARPINUS—OSTRYA	10	5	3	3				21	1.6

$$\text{Aggregate difference} = \sqrt{\Delta_1^2 + \Delta_2^2 + \Delta_3^2 + \Delta_4^2 + \Delta_5^2 + \Delta_6^2}$$

Thus the aggregate difference between *Alnus cordata* and *Alnus maritima* is calculated from the data in Table I as follows:

$$\sqrt{(7-7)^2+(0-0)^2+(4-3)^2+(5-5)^2+(2-2)^2+(1-1)^2}$$
$$=\sqrt{0+0+1+0+0+0}$$
$$=\sqrt{1} = 1.0$$

The difference between *Alnus cordata* and *Carpinus japonica* becomes:

$$\sqrt{(7-8)^2+(0-4)^2+(4-6)^2+(5-3)^2+(2-2)^2+(4-1)^2}$$
$$=\sqrt{1+16+4+4+0+9}$$
$$=\sqrt{34}$$
$$= 5.83$$

Analytically the magnitude of the difference is the length of a line between two points each of which is defined in six dimensions. Mathematically it would not be necessary to give the index a graphical interpretation, but many biologists find it easier to think geometrically than arithmetically.

In Table II, the magnitudes of the differences between the various species are tabulated and summarized. They are considered within sections of the genera, between sections within genera, and between genera. For the inter-specific comparisons all the possible combinations were calculated when the numbers of species in the genera under comparison were small. In the larger genera, 25 comparisons were chosen by chance, and the average calculated from these choices.

Table II shows a number of interesting facts:

1. The differences between genera are of greater magnitude than the differences within genera.

2. The differences between species within the same section are of relatively the same magnitude throughout the Betulaceae. The average difference in *Ostrya*, on the scale of the index, is 1.1; in *Betula*, 0.8; in *Carpinus*, 1.2; in *Corylus*, 0.8; in *Alnus* it is 1.0. This is an indication that the qualitative work of the taxonomists and morphologists who have dealt with the group has been surprisingly constant from genus to genus. This is particularly interesting in view of the fact that the six features used in computing the index are far from identical with those used in taxonomic work. Two of them indeed (Nos. 1 and 6) bear no direct relationship thereto.

Using the average distances between genera as obtained in the last column of Table II, a three-dimensional model was constructed. Just as the distance between any two points can be represented on a single straight line, but the distances between any three may require a plane for graphical representation, so in this problem we are entitled to five dimensions to show the relationships between our six genera. Fortunately the relationships are simple enough so that three dimensions will give a working approximation. A study of the model reveals sev-

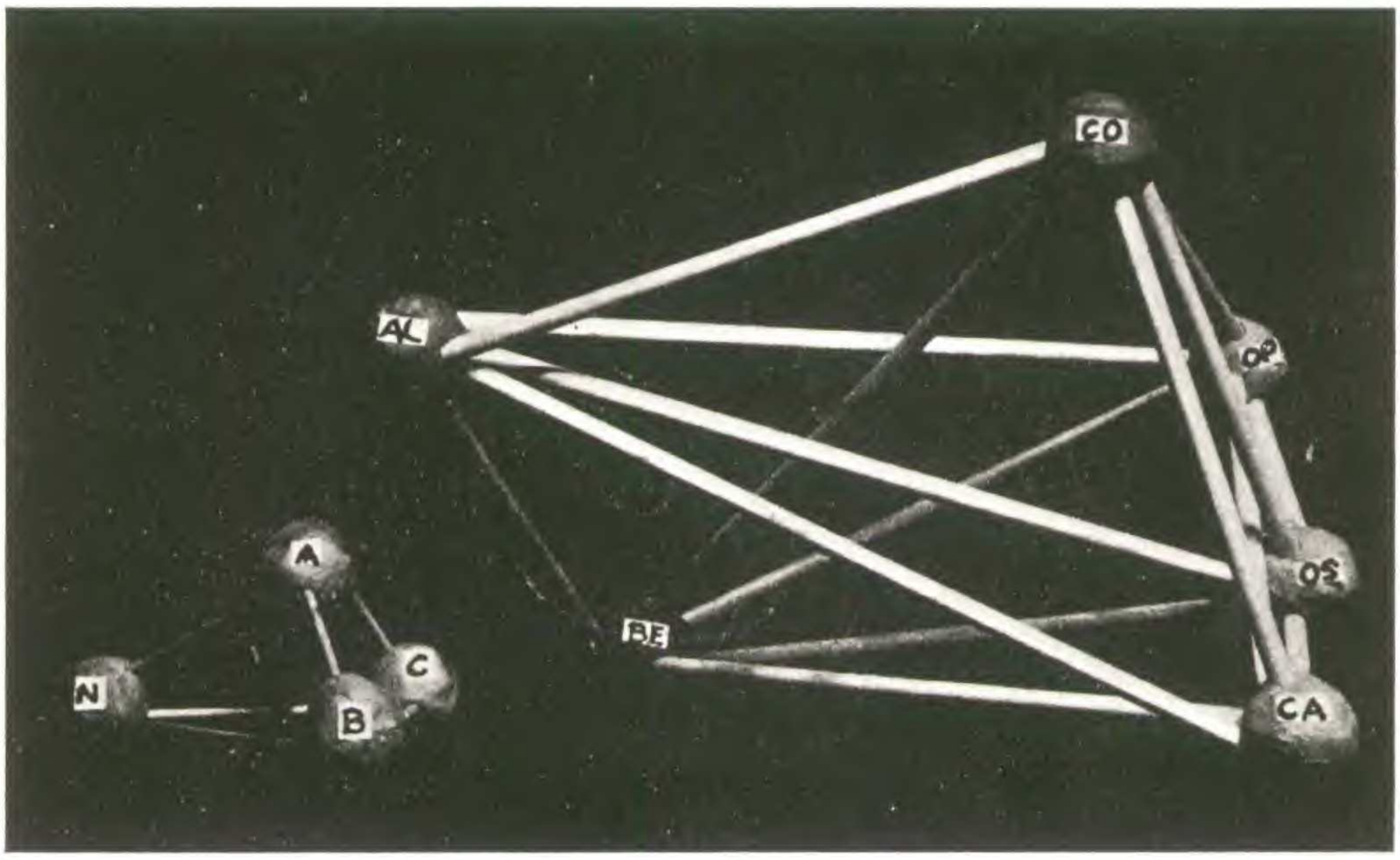

FIGURE 1. Models showing the comparative distances between the genera of the Betulaceae and the sub-sections of the genus *Betula*. For the larger model, AL, *Alnus;* CA, *Carpinus;* CO, *Corylus;* OP, *Ostryopsis;* OS, *Ostrya*. For the smaller model, N, §§*Nanae;* A, §§*Albae;* B, §§*Acuminatae;* C, §§*Costatae*.

eral interesting points (Fig. 1). It should be borne in mind that the lines connecting genera in the model are not meant to diagram phylogenetic lines of development. They indicate nothing more than comparative distances between genera as determined by the method developed above.

(1) There are two groups of genera, *Carpinus* — *Ostrya* — *Ostryopsis* at one end of the family and *Alnus* — *Betula* at the other. *Corylus* occupies a position off at one side and not clearly to be identified with either of the other groups.

(2) *Carpinus, Ostrya,* and *Ostryopsis* form a straight-line sequence.

That is, the change from *Carpinus* to *Ostrya,* carried on still further in the same direction, will reach *Ostryopsis.* The model, of course, gives no hint of the direction of this apparent phylogenetic sequence; whether it is from *Carpinus* to *Ostryopsis,* or *vice versa.*

Betula was the only genus for which the intersectional figures were complete enough to warrant detailed comparison between sections and genera. A model of the sub-sectional relationships in *Betula* on the same scale as the other model is shown in Figure 1. The magnitude of sub-sectional differences in *Betula* is clearly less than that of the differences between *Betula* and its closest relatives. The *Nanae* sub-section, however, as measured by this index shows a divergence from the other three sub-sections greater than that between *Ostrya* and *Carpinus.*

SUMMARY

(1) The qualitative nature of taxonomic units is briefly discussed.

(2) A quantitative method is advanced for dealing with these units, and generic and specific differences in the Betulaceae are compared. It is shown that the latter are much smaller, and that they are approximately equal in average magnitude from genus to genus.

(3) Models are constructed showing on the same scale the comparative divergence between the genera of the Betulaceae and of certain sub-sections in the genus *Betula.*

LITERATURE CITED

Abbe, Ernst C. (1933). The inter-relationship of the genera of the Betulaceae, based on anatomical studies of the inflorescence, the flowers, and the secondary xylem. (Thesis, Harvard University [MS.].)

Anderson, Edgar & Whitaker, Thomas W. (1934). Speciation in Uvularia. (Jour. Arnold Arb. **15**:28–42.)

Woodworth, R. H. (1931). Polyploidy in the Betulaceae. (Jour. Arnold Arb. **12**:206–217.)

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